Ecological Modelling 390 (2018) 79–87

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Using macroecological constraints on spatial biodiversity predictions under climate change: the modelling method matters

Mirko Di Febbraro[a,*], Manuela D'Amen[b], Pasquale Raia[c], Davide De Rosa[a], Anna Loy[a], Antoine Guisan[b,d]

[a] Department of Biosciences and Territory, University of Molise, Contrada Fonte Lappone, 86090, Pesche, Isernia, Italy
[b] Department of Ecology and Evolution, University of Lausanne, Biophore building, 1015, Lausanne, Switzerland
[c] Department of Earth Sciences, Environment and Resources, University of Naples Federico II, L.go San Marcellino 10, 80138, Naples, Italy
[d] Institute of Earth Surface Dynamics, Geopolis, University of Lausanne, 1015, Lausanne, Switzerland

ARTICLE INFO

Keywords:
SESAM framework
Community ecology
Macroecological models
MEM
Species distribution models
SDM

ABSTRACT

The prevailing method for estimating the potential impact of future climate change on biological communities is to stack binary predictions from species distribution models (binary stacked species distribution models, bS-SDM). However, it has been argued that bS-SDM may overestimate species richness and, hence, community composition. Alternative approaches, such as SESAM ('Spatially Explicit Species Assemblage Modelling'), explicitly incorporate limits to species richness, preventing overestimation. We compared richness and taxonomic composition estimates as predicted by SESAM and bS-SDM for Mediterranean bird communities both in the present day and as projected in the future under simulated climate change scenarios. We trained single-species distribution models (S-SDM) and direct macroecological richness models (MEM) for 81 bird species, using climate, topographic, land-use and human-pressure indicators as predictors. Then, we compared and evaluated the models' predictions. Species richness as predicted by bS-SDM was more accurate than under SESAM for present-day communities. Taxonomic composition was well predicted under both methods. However, we detected significant differences in future projections. Under bS-SDM, increased suitable area for a number of species leads to important changes in community composition and predicts higher levels of diversity in the future. In stark contrast, SESAM predicts lower species richness in the future and strong homogenization of bird communities across space. This study shows how the choice of the modelling approach drives substantially different expectations about future community composition under climate change. We therefore recommend contrasting predictions generated under different modelling approaches to gain better understanding of possible future scenario of biodiversity change. In addition, trasferability tests (i.e. hindcasting to past or predicting from the past to the present) should be used to effectively compare S-SDM and SESAM predictive abilities.

1. Introduction

Global climate change will affect life-history, abundance, distribution and survival of a wide array of organisms (Knudsen et al., 2011; Maiorano et al., 2011; Parmesan, 2006; Schaefer et al., 2008). Species inability to respond to changing environmental conditions may result in declining population numbers and eventually extinction (Parmesan, 2006). Alternatively, species may track their most favourable habitats (Maggini et al., 2011; Raia et al., 2012; Schaefer et al., 2008), or even evolve new, ad hoc, adaptations (Bradshaw and Holzapfel, 2006). At the community-level, habitat tracking and local extinctions are predicted to increase species turnover (Schaefer et al., 2008), and to alter ecosystem functioning (Barry et al., 1995).

Until now, the prevailing method to assess the potential impact of climate change on community composition has been using binary stacked species distribution models (bS-SDM). Under bS-SDM, binary predictions derived from SDM trained under current conditions and projected to the future (Ferrier and Guisan, 2006; Guisan and Thuiller, 2005) can be stacked to predict present and future species richness, and assess changes over time. A common problem with bS-SDM is the overprediction of species richness, which may hamper accurate composition estimates in present-day communities (Dubuis et al., 2011; Guisan and Rahbek, 2011; Hortal et al., 2012; Calabrese et al., 2014; Cord et al., 2014; D'Amen et al., 2015a; but see Mateo et al., 2012;

* Corresponding author.
E-mail address: mirkodifebbraro@gmail.com (M. Di Febbraro).

https://doi.org/10.1016/j.ecolmodel.2018.10.023
Received 17 July 2018; Received in revised form 23 October 2018; Accepted 28 October 2018
Available online 12 November 2018
0304-3800/ © 2018 Elsevier B.V. All rights reserved.

D'Amen et al., 2015b). However, recent papers also provided examples where predictions of single-species distribution (S-SDM) yielded accurate estimations of species richness and composition, suggesting that richness overprediction by bS-SDM may not necessarily be expected (Mateo et al., 2012; D'Amen et al., 2015b). In particular, it has been argued that both the identity and number of species in a local assemblage tend to be more accurately predicted by bS-SDM in stressful (i.e. non-productive) habitats (Pellissier et al., 2012; Pottier et al., 2013), and where climate is the main determinant of species distribution and richness (Mateo et al., 2012). Similarly, the inclusion of predictors serving as proxies for resource availability helps reducing the problem of richness overestimation (D'Amen et al., 2017a, 2015b). However, little is known about whether richness overprediction might affect future S-SDM projections of community composition.

A number of alternatives or improvements to bS-SDM have been proposed in the scientific literature (D'Amen et al., 2017b; Fernandes et al., 2013; Laughlin et al., 2012; Mokany et al., 2012). Among them, SESAM ('Spatially Explicit Species Assemblage Modelling', Guisan and Rahbek, 2011), proved especially accurate (D'Amen et al., 2017a, 2015a). SESAM couples SDM to macroecological constraints and assembly rules (D'Amen et al., 2017a, 2015b, 2015a). This is meant to fix the problem that the simple stacking of individual species predictions ignores the effects of species interactions on local richness (Ferrier and Guisan, 2006; Gleason, 1939), such as competitive exclusion and niche-preemption (Callaway, 1997). Under SESAM, independent limits are imposed to local species richness, so that more realistic scenarios for community assemblage could theoretically emerge (Guisan and Rahbek, 2011; but see Mateo et al., 2017).

Herein, we explored the performance of bS-SDM and SESAM in predicting community composition under both current and future climatic conditions for bird communities in Southern Italy. Specifically, we hypothesized that i) SESAM would predict present-day community properties more accurately than bS-SDM; ii) bS-SDM and SESAM would provide different predictions of community richness and composition under climate change; iii) SESAM would predict a more ecologically plausible response by communities to climate change than bS-SDM.

2. Material and methods

Our analytical framework starts by applying bS-SDM and SESAM to bird communities within a geographically restricted but environmentally highly heterogeneous area representative of the typical Mediterranean habitats (Fig. 1). We proceeded by calibrating and stacking S-SDM to build bS-SDM community richness and composition. Since the study area covers just a small portion of the analysed species global ranges, S-SDM were fitted using a hierarchical structure, integrating global and regional scales (Di Febbraro et al., 2015; Smeraldo et al., 2017) in order to avoid truncated response curves (and associated truncated niche) that could bias the predictions, especially when models are projected in space and time (Barbet-Massin et al., 2010; Guisan et al., 2017; Raes, 2012). Accordingly, a first set of models was fitted with data on the global species range (global SDM) and global bioclimatic variables. Then regional models were fitted with regional data and predictors, and information from the global models were used to refine these predictions (Gallien et al., 2012). The SESAM framework was then based on these regional models and included the following steps (Guisan and Rahbek, 2011; Fig. 1): step 1) selecting the pool of species to build the community (i.e. the species source pool); step 2) calibrating and stacking S-SDM (i.e. selecting the abiotic habitat species pool); step 3) using species richness predictions as constraint on the community (i.e. setting macroecological constraints); step 4) applying ecological assembly rules (i.e. biotic filtering). In particular, we calculated macroecological constraints in step 3 both by summing the rough occurrence probabilities (considering five decimal places) obtained from the single-species distribution (pS-SDM; Dubuis et al., 2011) and by fitting macroecological models (MEM; Vincent and Haworth, 1983; see also Dubuis et al., 2011). Consequently, we derived two alternative implementations of SESAM considering richness predictions either by MEM (SESAM_MEM) or by pS-SDM (SESAM_prob; Fig. 1). Subsequently, the evaluation scores of SESAM_MEM and SESAM_prob were compared with those obtained from the application of the bS-SDM approach. Finally, after projecting S-SDM and MEM under two different climate change scenarios (A2 and B1, IPCC, 2007; Fig. 1) for 2070, we compared the outcomes of the three implemented modelling approaches, i.e. SESAM_MEM, SESAM_prob and bS-SDM.

2.1. bS-SDM implementation

We selected bird communities from Southern Italy, over a surface area extending from the Tyrrhenian to the Adriatic Seas, at altitudes varying from the sea level to 1900 m a.s.l. (Fig. S1). The area is largely covered by agricultural mosaics, and encompasses a great variety of other habitat types, from coastal wetlands to mountain forests. The species dataset includes presence observation derived from field surveys within the "Italian Breeding Bird Monitoring Programme" (MITO2000 Project; Fornasari et al., 2002; Chiatante and Meriggi, 2016; Stephens et al., 2016; Chiatante, 2017; see Appendix S1 for details). From the initial dataset (which includes 134 species), we discarded all species with less than 15 occurrences. The final dataset includes 81 species (Table S1) occurring throughout 1010 cells. Since the study area largely occurs within the historical ranges of all species, without any evidence of dispersal limitation, we considered these species to form an unique species source pool (see also D'Amen et al., 2015b, 2015a and Guisan and Rahbek, 2011). The selection of species source pool represented a common step to both bS-SDM and SESAM approaches (Fig. 1).

For global SDM calibration, we initially considered the 19 WORLDCLIM predictors at a spatial resolution of 2.5 arc-minutes (ca. 5 km; Hijmans et al., 2005; Table 1; Appendix S1). As for regional SDM, the initial set of covariates included the 19 WORLDCLIM predictors, five topographic variables in combination with a coarse habitat classification (11 classes) and a human pressure index (see Table 1 and Appendix S1 for further details), all rasterized at a resolution of 1 km. For both regional SDM and MEM, we assessed the effect of model extrapolation on the values of predictor variables lying outside the training range, by calculating the Multivariate Environmental Similarity Surface (MESS; Appendix S3), following Elith et al. (2010).

To avoid model overfitting and allow species with small sample size to be modelled, regional SDM were trained by ensembling small (sub) models (ESM; Breiner et al., 2015; Lomba et al., 2010; Di Febbraro et al., 2017) based on reduced subsets of the initial predictors (Appendix S1). bS-SDM obtained in this step were then used to build current and future community predictions (see Fig. 1 and Appendix S1). Calibration and stacking of S-SDM is a common step to both bS-SDM and SESAM approaches. In the latter, stacked species distributions were additionally constrained by the macroecological richness predictions and ecologically assembly rules were applied (Fig. 1). All models, global and regional, were evaluated by randomly splitting occurrence datasets into a 70% sample, for models calibration, and a remaining 30%, to evaluate model predictive performance, repeating the procedure 10 times and averaging the results. The predictive performance of each model was assessed by measuring the area under the receiver operating characteristic curve (AUC; Hanley and McNeil, 1982) and the maximized true skill statistic (maxTSS; Allouche et al., 2006).

2.2. SESAM implementation

Both bS-SDM and SESAM imply selecting a pool of species and fitting/stacking single-species distributions, which were outlined in the previous sections. Here, we will describe the remaining steps, i.e. setting macroecological constraints and applying ecological assembly rules.

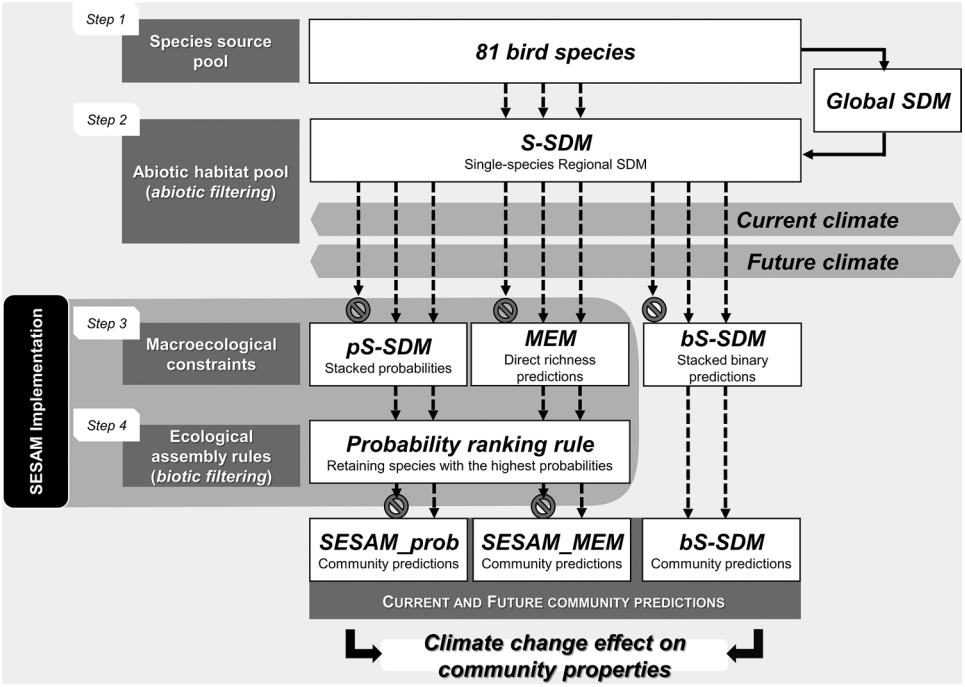

Fig. 1. Flowchart summarizing the modelling framework followed in the study. Forbidden symbols indicate that a given species was filtered out at a particular step of the procedure, without proceeding further in shaping the final predicted community.

Table 1
Predictors used in global and regional SDM.

Predictor	Cell size (km^2)	Source
Global scale		
Mean diurnal range	5	WORLDCLIM database
Mean temperature of wettest quarter		
Mean temperature of driest quarter		
Precipitation of driest month		
Precipitation seasonality		
Precipitation of warmest quarter		
Precipitation of coldest quarter		
Regional scale		
Temperature annual range	1	WORLDCLIM database
Precipitation of warmest quarter		
Human footprint index		WCS & CIESIN database
Slope		Derived by WORLDCLIM DEM
Topographic position index		
Euclidean distance from Rock faces		
Euclidean distance from Water flows		Institute for Environmental Protection and Research
Euclidean distance from Arable land		
Euclidean distance from Artificial surfaces		
Euclidean distance from Forests		
Euclidean distance from Open spaces with little or no vegetation		
Euclidean distance from Pastures		
Euclidean distance from Permanent crops		
Euclidean distance from Scrub or/ and herbaceous vegetation associations		
Euclidean distance from Water bodies		

2.2.1. Setting macroecological constraints

Under SESAM, macroecological constraints are set to limit species richness in the S-SDM. As specified above, we calculated species richness by pS-SDM and MEM. MEM takes the number of species occurring at each cell (observed richness) as the response variable, and relate it statistically to the regional predictors (see Table 1). We used zero-inflated Poisson regressions to account for the excess of zeroes in the dataset (~26%; Lambert, 1992), and implemented a variable selection procedure to select predictors (Appendix S2). The accuracy of the models was evaluated with a 10-fold cross-validation procedure with two metrics: the Spearman rank correlation coefficient and the mean absolute error (MAE; Steinmann et al., 2009; Dubuis et al., 2011; D'Amen et al., 2017a, 2017b). The 10 resulting richness predictions were averaged and used to produce local species richness constraints. Such constraints were estimated under present day conditions and projected to the year 2070, under IPCC's A2 and B1 climate change scenarios (IPCC, 2007).

2.2.2. Accounting for ecological assembly rules

Where species richness is overestimated, the excess number of species has to be deleted in order to fit to the macroecological constraint. To do so, we used alternatively MEM or pS-SDM richness estimates (Fig. 1) as the constraint. At each cell, we ranked individual species according to their occurrence probability predicted by S-SDM, from highest to lowest. We then retained those species with highest probabilities until the number of species predicted by MEM or pS-SDM was reached, and discarded the excess specices ("Probability ranking" rule; D'Amen et al., 2015a, D'Amen et al., 2017a,b).

2.3. Evaluating bS-SDM and SESAM predictive accuracy

Performances of bS-SDM and SESAM approaches to predict current distributions were assessed by calculating three different evaluation metrics: richness deviation, prediction success and Sørensen similarity index (in composition) between predicted and observed communities. Richness deviation metric indicates the difference between predicted and observed species richness; prediction success quantifies the proportion of species correctly predicted as present or absent. The Sørensen similarity index describes the compositional similarity between observed and predicted communities. Values closer to zero for the former and closer to one for the latter two indicate high predictive accuracy

(D'Amen et al., 2015a; Pottier et al., 2013).

2.4. Effects of climate change on the predicted communities

To allow a comprehensive evaluation of prediction differences under climate change, we measured changes in species distribution (extent and shift) and community structure (species richness and diversity). Specifically, we considered changes in five community dimensions: i) total number of species predicted in the study area; ii) extent and shift of future species distribution; iii) species richness at the level of individual cells; iv) differences in species composition and v) γ-diversity (i.e. within-landscape diversity). The total number of species predicted in the area was calculated by grouping the species according to their degree of "rarity" in the area. We created four rarity classes according to the percentage of the total area where the species were predicted to occur (i.e. 0–5%; 5–25%; 25–50% and > 50%). For each species, the extent of the predicted distribution in 2070 was expressed as the percentage of the present-day distribution, whereas shift was expressed as the percentage of overlap with the current predicted distribution (Huntley et al., 2008). In addition, we compared the differences in extent and shifts of predicted future distributions between resident and migratory species. Since an altered balance between residents and migrators has been observed as one of the most evident effects of climate change on birds (Lemoine et al., 2007; Van Turnhout et al., 2010), we calculated this "phenological" metric in order to assess the ecological plausibility of our future predictions in comparison to independent, well-documented patterns and expert-based expectation. The Sørensen dissimilarity index (i.e. 1 – Sørensen similarity index, see above) was used to quantify the differences in species taxonomic composition at cell-level between the current and future (2070) communities. The values of the index were split into positive and negative components, depending on the alterations in the composition of the 2070 communities deriving from an increase or a decrease in the species richness at the cell-level. Finally, we calculated the Sørensen dissimilarity index between cells pairs taken from current and 2070 predictions separately, to quantify the γ-diversity for current and future predicted communities (see Appendix S4 for further details).

3. Results

3.1. Species distribution models

Both global and regional SDM reached good predictive performances overall (*sensu* Landis and Koch, 1977; Swets, 1988). AUC for the global SDM ranged between 0.913 and 0.998, with a mean value of 0.954 (SD = 0.024), whereas maxTSS ranged between 0.642 and 0.966, with a mean value of 0.793 (SD = 0.083). AUC values for the regional SDM ranged between 0.838 and 0.998, with a mean of 0.940 (SD = 0.043), whereas maxTSS values ranged between 0.557 and 0.993, with a mean of 0.782 (SD = 0.125).

3.2. Species richness accuracy

Species richness predicted by bS-SDM was correlated with the observed richness with a Spearman $\rho = 0.731$ (Fig. 2a). The regression line through the scatter plot (adjusted-$R^2 = 0.567$) showed an intercept of 7.532 ($p < 0.01$) and a slope of 0.770 ($p < 0.01$), suggesting that observed species richness was sligthly overestimated (although this pattern becomes negligible for the species-richest sites). In addition, a positive prediction bias was observed, with a mean richness deviation of 5.164 and a MAE of 5.372.

The species richness predictions calculated with MEM achieved a much lower correlation with the observed richness, with a mean Spearman $\rho = 0.420$ (SD = 0.050) resulting from the cross-validation replicates (Fig. 2b). Sites with the lowest observed species richness showed moderate levels of overprediction, whereas plots with an observed richness > 10 appeared to be markedly underestimated. The patterns of both overprediction and underprediction of the observed species richness showed by MEM were confirmed by the regression line through the scatter plot (adjusted-$R^2 = 0.131$), which had an intercept of 9.775 ($p < 0.01$) and a slope of 0.055 ($p < 0.05$). In addition, a negligible prediction bias (mean deviation = – 0.012; MAE = 4.828) was observed.

The richness predictions obtained by pS-SDM were better correlated with the observed richness with a Spearman $\rho = 0.700$ (Fig. 2c). However, the regression line drawn through the scatter plot had an intercept of 18.584 ($p < 0.01$) and a slope of 0.307 ($p < 0.01$), thus showing a stronger overprediction of the observed species richness than with bS-SDM. In addition, species-richest and species-poorest sites were shown to be markedly under- and over underestimated respectively (although less than for MEM). A positive prediction bias was observed, with a mean richness deviation of 11.406 and a MAE of 11.632.

Spatial predictions of current species richness by bS-SDM, MEM and pS-SDM are shown in Fig. S2.

3.3. Species composition accuracy

The species composition predicted by both bS-SDM and SESAM implementations showed a fair to good predictive accuracy (Fig. 2e–f). The application of SESAM did not significantly improve (Wilcoxon-test, $\alpha = 0.05$) the predictions obtained by the simple bS-SDM according to the Prediction Success index (Fig. 2e). The lowest score was obtained by SESAM_prob, which had a prediction success index < 0.9, less accurate than bS-SDM in predicting species richness (Fig. 2e). This pattern was even more evident when considering the Sørensen similarity scores, which showed that both SESAM_MEM and SESAM_prob generated predictions of significantly lower accuracy (Wilcoxon-test, $\alpha = 0.05$) than bS-SDM (Fig. 2f). As bS-SDM and SESAM_MEM had the highest predictive accuracy, we hereafter only show predictions generated with these two approaches (for SESAM_prob, see results in Fig. S3-S4).

3.4. Effects of climate change on the predicted communities

Spatial predictions of future species richness by bS-SDM, MEM and pS-SDM are shown in Fig. S2. Remarkable differences were observed in the number of species predicted in the study area by bS-SDM and SESAM_MEM. While this parameter was predicted by bS-SDM to remain constant between the current time and 2070 regardless of the climate change scenarios (Fig. 3a), it showed a strong decrease in 2070 according to SESAM_MEM, with a loss of more than 20 species (Fig. 3f). Different outcomes of bS-SDM and SESAM_MEM were observed in the predicted extent and shift of the species distributions in 2070. Indeed, bS-SDM predicted a decrease in extent of less than 26% and 23% of the species under A2 and B1 scenarios, respectively (Fig. 3b–c), with a preponderance of resident species (Fig. 3d). Only few species (15%), mainly to be found among the less common and the rarest, were predicted to shift their distribution more than 50% under both scenarios (Fig. 3b-c), with a more pronounced effect on migrators (Fig. 3e). On the contrary, SESAM_MEM predicted 79% and 75% of the species to reduce their 2070 predicted distribution under A2 and B1 scenarios respectively, with a 30% completely losing their suitable areas under both scenarios (Fig. 3g–h). Moreover, SESAM_MEM outcomes showed a full range displacement for at least 30% and 35% of the species under A2 and B1 scenarios respectively, all represented by the less common and rarest, migratory species (Fig. 3g–h and i–l).

Predictions by bS-SDM and SESAM_MEM showed diverging patterns of predicted species richness per cell. It would increase in 2070 according to the bS-SDM outcomes (Fig. 4a–b), whereas such effect was less evident in the communities predicted by SESAM_MEM (Fig. 4c-d). The predictions of both bS-SDM and SESAM_MEM showed relevant alterations in species composition within cell, regardless of the scenarios. Indeed, the communities predicted by bS-SDM exhibited a

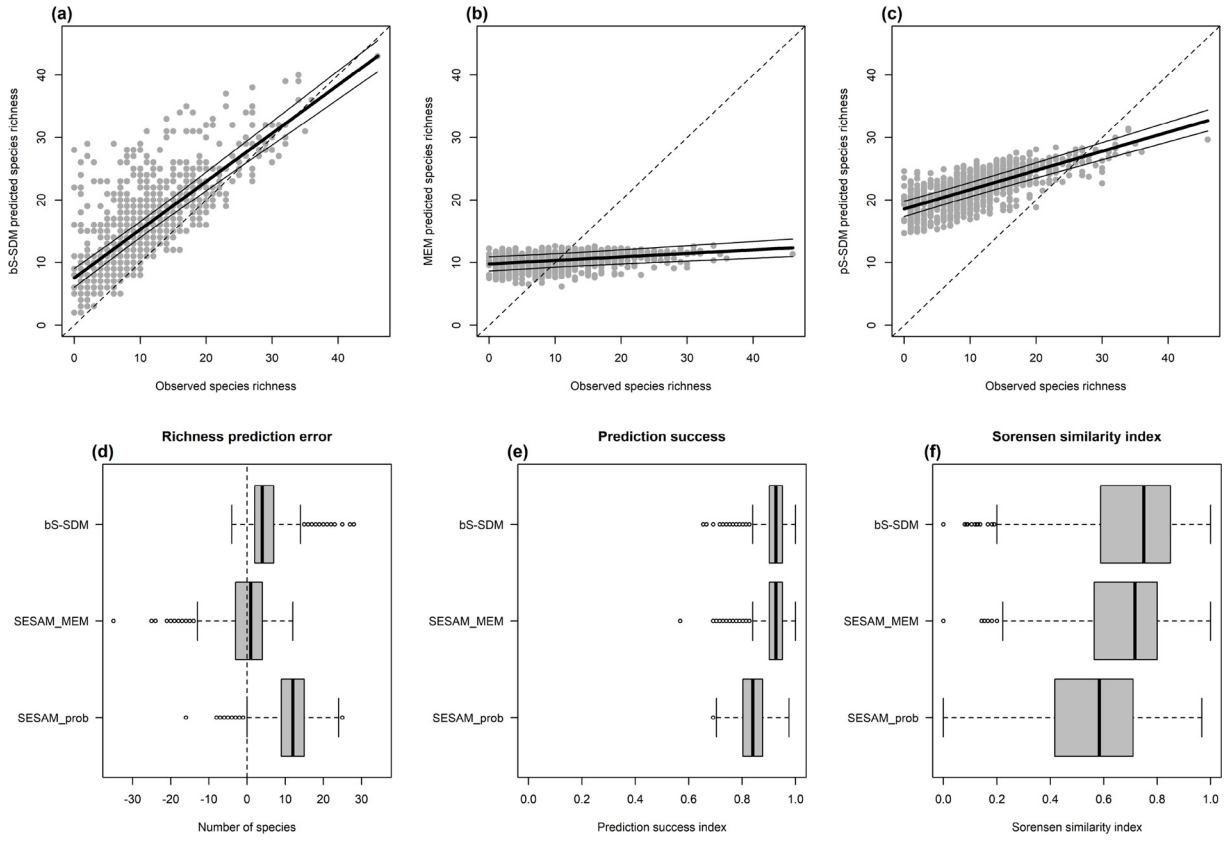

Fig. 2. Predictive accuracy of the community properties. Upper row: predicted species richness plotted against the observed data for (a) bS-SDM, (b) MEM and (c) pS-SDM. The dashed line shows a perfect correspondence between observed and predicted species richness, while the solid, thick line corresponds to a linear regression and the thin lines indicate its 95% confidence interval. Bottom row: values of richness deviation (d), prediction success (e) and Sørensen similarity index (f) for the communities predicted by bS-SDM and the two SESAM implementations.

change in species composition of approximately 60% due to both increase and decrease of species richness in different cells (Fig. 4a-b). Such trend proved even stronger in the communities predicted by SESAM_MEM, which showed a change in their species composition of ca. 70% due to increase, and 80% due to decrease of species richness, under all the scenarios (Fig. 4c-d).

Finally, climate change is predicted to have negligible effect on γ-diversity by bS-SDM (Fig. 4a-b), whereas γ-diversity was predicted to decrease in 2070 according to SESAM_MEM, regardless of the climate change scenarios (Fig. 4c-d).

4. Discussion

4.1. Community-level predictions at current time

Our results showed that both bS-SDM and SESAM approaches can predict species richness and composition of bird communities with overall fair to good accuracy under current climatic conditions. The binarized bS-SDM predictions showed better overall correlation with observed richness than pS-SDM and MEM predictions along the whole richness gradient (Fig. 2), predicting much better the low and high species richness values in particular. For MEM, it confirms previous findings suggesting that MEM is not the most appropriate method to predict extreme (low or high) richness values (Algar et al., 2009; Dubuis et al., 2011; Newbold et al., 2009). The not so strong relationship between observed richness and values predicted by MEM has been noted elsewhere (Algar et al., 2009; Dubuis et al., 2011; Guisan and Theurillat, 2000; Thuiller et al., 2006) and is particularly marked here. It can be linked to the fact that MEM, by modelling the mean, is not well-designed to capture strong richness variation around this mean. Furthermore, producing an optimal macroecological constraint across a heavily anthropogenized study area like ours might be objectively difficult. This should be considered with care when using MEM within a SESAM framework.

It is also noteworthy that bS-SDM provided more accurate richness predictions than pS-SDM. Prediction errors under bS-SDM remarkably decreased in sites with high observed richness, resulting in a nearly negligible underestimation of the species-richest sites, a trend opposite to the findings in Algar et al. (2009) and Calabrese et al. (2014). The latter suggested that the systematic richness overestimation reported for bS-SDM is due to the binarization thresholding scheme largely adopted so far for stacking SDM outputs (as e.g. used in Barbet-Massin et al., 2010; Dubuis et al., 2011). Here, however, we observed the opposite pattern: using a threshold reduced the overprediction compared to pS-SDM, leading bS-SDM to perform better overall. In particular, the thresholding method used here accounts for differences in prevalence among species (Liu et al., 2005). In our case, the vast majority of species were characterized by low prevalences (i.e. 0.110 ± 0.017), leading to overall high threshold values (Fig. S5). Such result appeared coherent with the evidence in Mateo et al. (2012), which highlighted how choosing a thresholding method able to control for overprediction, coupled with highly performing single-species SDM ensembles, may yield accurate richness predictions by bS-SDM. This interpretation is also in accordance with D'Amen et al. (2015b), who tested a number of thresholding methods to binarize the single-species SDM ensembles and reported that bS-SDM derived from highly accurate SDM are able to correctly predict species richness for insect species (but not for plants; see D'Amen et al., 2015a), irrespectively of most of the thresholding schemes applied. Therefore, the taxonomic group and the number of species being modelled could also matter.

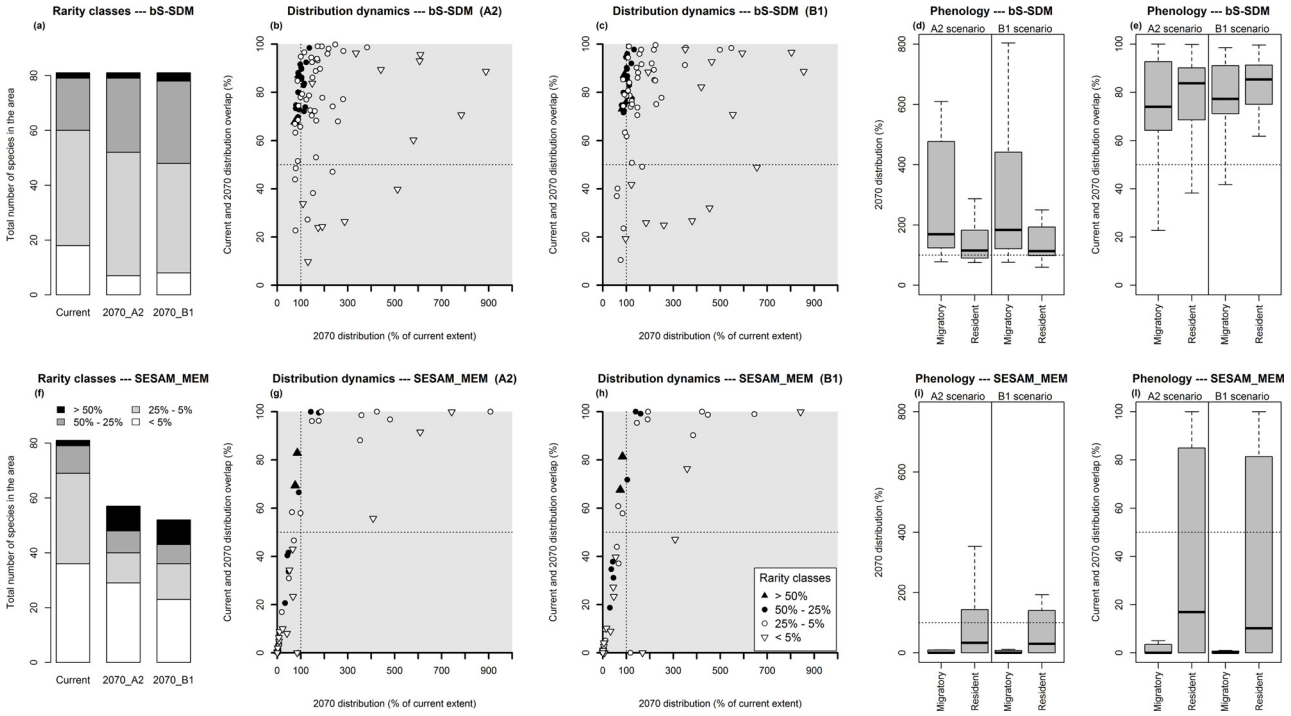

Fig. 3. Effect of climate change on number of species and potential distributions of the predicted communities. The first line reports the bS-SDM predictions, while the second refers to SESAM_MEM. Barplots (a, f) depict the current and future number of species in the study area. Grey-scale colors refer to the four rarity classes (see text): 0–5% (white); 5–25% (light grey); 25–50% (dark grey) and > 50% (black). Scatterplots (b–c, g–h) show the extent of the 2070 predicted distributions against its overlap with the current distributions (both expressed as percentage of the current distributions). Dotted lines indicate the 'no-change' value of 100% for the extent (vertical) and a shift of 50% (horizontal) of the future distributions. Black symbols refer to the upper two rarity classes, while white symbols to the lower two, with triangles indicating the most common and rarest classes, respectively. Boxplot (d–e, i–l) depict the extent and overlap of 2070 distributions partitionated between residents and migrators.

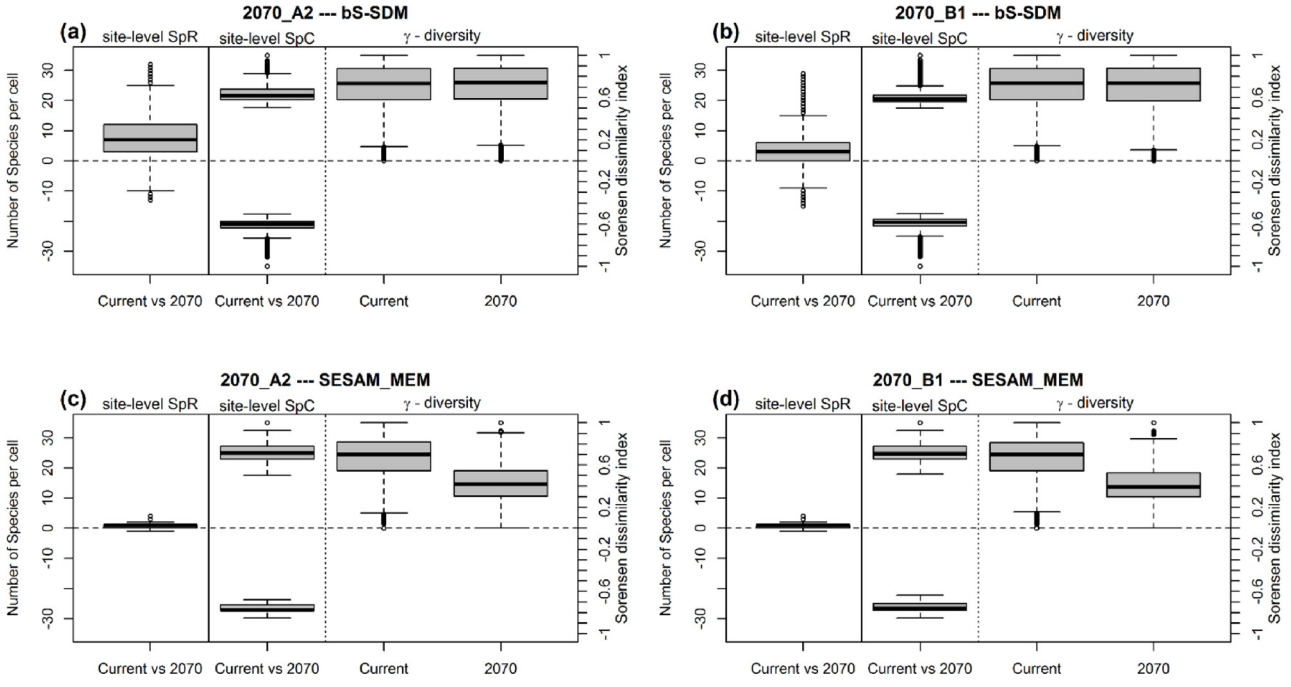

Fig. 4. Effect of climate change on richness, composition and diversity of the predicted communities. First line report the bS-SDM predictions, while the second refers to SESAM_MEM. The first boxplot of each panel depicts the balance between 2070 sites with gained and lost species richness. The second boxplot shows the differences between current and 2070 species composition at site-level due to increase (upper part) and decrease (lower part) of species richness (see text). The last two columns refer to the γ-diversity of current and 2070 communities, respectively.

Overall, good predictions of community composition were obtained through both bS-SDM and SESAM implemented with the MEM richness prediction in the current conditions. In particular, the bS-SDM prediction was the best according to the Sørensen index. The implementation of SESAM coupled with the pS-SDM prediction had the lowest performance, likely due to the higher richness overprediction in pS-SDM. The decrease in compositional accuracy due to richness overprediction has been described to date only for bS-SDM predictions (D'Amen et al., 2015a; Dubuis et al., 2011), while our results support the idea that the same may apply under alternative approaches.

4.2. Predicted effects of climate change on the communities

Overall, bS-SDM predicted less severe impacts of climate change on the analysed communities in 2070 than SESAM_MEM. Under bS-SDM, the bird species (and especially migrators) showed a tendency to increase and moderately shift their distribution ranges in 2070, while none of the species was predicted to lose suitable range altogether. This result agrees with studies suggesting European birds will extend their distribution towards the North following climate change (Huntley et al., 2006; Maggini et al., 2011), although a predominant increase in the future distribution of migratory species was not consistently supported in the literature (Angert et al., 2011; Knudsen et al., 2011; Lemoine et al., 2007; Tingley et al., 2012; Van Turnhout et al., 2010). If true, this widening of future species distributions predicted by bS-SDM will lead to increased average species richness per cell in 2070. In addition, these range modifications might lead to strong alteration of community composition at local scale and to the formation of assemblages without present-day analogues (Böhning-Gaese and Lemoine, 2004; Knudsen et al., 2011).

The change in community composition predicted by SESAM offers a very different scenario from bS-SDM in 2070. In particular, SESAM_MEM predicted that the rarest migratory species will undergo more severe climate-driven distributional changes than resident species, thus substantially contradicting bS-SDM results. Similar expectations derive by taking into account the nature of interspecific interactions between migrators and residents (Knudsen et al., 2011), predation risk (Bretagnolle and Gillis, 2010; Niehaus and Ydenberg, 2006) and parasitism (Douglas et al., 2010; Möller et al., 2011). In addition, the substantial de-structuration of current communities and the reduction in within-landscape diversity predicted by SESAM_MEM agrees with expert-based expectations. In particular, mild winters are expected to decrease the proportion of migrants and increase the survival of residents, resulting in the former experiencing increased competition for resources upon arrival (Lemoine and Böhning-Gaese, 2003; Schaefer et al., 2008), and ensuing population decline (Knudsen et al., 2011; O'Connor, 1990). Such climate change-induced dynamics are said to cause severe alterations in species composition, ultimately leading to taxonomic homogenization at the local scale (Böhning-Gaese and Lemoine, 2004; Cassey et al., 2007; Diffenbaugh et al., 2007; Morelli et al., 2016). It was shown that modelling approaches taking biotic interactions into account tend to give higher extinction risk estimates than predictions based on models fitted with environmental predictors alone (Araújo and Luoto, 2007; Hein et al., 2012; Hof et al., 2012). SESAM_MEM seems to be consistent with this general tendency.

Future projections could further be improved by considering potential changes in land-use. Although, the relevance of land-use change for Mediterranean birds has already been documented (Moreira and Russo, 2007; Seoane et al., 2006; Sirami et al., 2008), its interaction with climate change deserves further investigation (Sirami et al., 2017) and there is a substantial lack of high resolution, long term, land-use change scenarios for Southern Italy. Still, our approach was not able to consider possible local extinctions. Since we considered as extinct in the area only those species predicted to entirely lose their suitable habitats, the number of local extinctions could have been underestimated (Allen et al., 2001; Brito and Grelle, 2006). Lastly, we did not consider possible colonizers from adjacent regions or from other continents (i.e. invasive species), which could immigrate into the study area tracking the climate change, thus further altering the considered bird community (Barbet-Massin et al., 2010; Schaefer et al., 2008).

5. Conclusion

If prediction accuracy under current climatic conditions is the goal, the traditional, simpler, widely-used bS-SDM approach proved at least as accurate as SESAM in predicting species richness and composition of bird communities in Southern Italy. However, bS-SDM and SESAM_MEM delivered significantly distinc predictions under the 2070 scenario. By considering environmental factors alone (bS-SDM), the present-day range of most species would increase in size and expand northwards, keeping local species diversity high. On the contrary, under SESAM, the inclusion of macroecological constraints and assembly rules leads to the alteration of the natural balance between migratory and resident species, biotic homogeneization, and a severe impact of climate change on species diversity. Considering expert-based predictions as true and admitting current observations on bird community change will hold true in the future, SESAM provided more realistic effects of climate change on the structure of bird communities, such as the higher sensitivity of migratory birds compared to residents, and the substantial homogenization of community structure (Böhning-Gaese and Lemoine, 2004; Cassey et al., 2007; Diffenbaugh et al., 2007; Gilman et al., 2010; Morelli et al., 2016).

Accurate predictions under climate change are challenging because they are sensitive to major uncertainties, like the chance that species will track their suitable habitat at the same pace as the climate change, or will adapt to new biotic interactions, as well as unpredictable effects coming by the interplay of multiple global change drivers (i.e. land-use change). Such uncertainties hamper our understanding of how species will react to non-analogous future environmental conditions, whereby the drivers of change (climate change, land-use change, pollution, etc.) will likely accelerate to levels which species and biological communities have never experienced in the last centuries. That said, our results further question the ability to predict community evolution under climate change and highlight the need for further investigations on community modelling to more comprehensively describe and quantify the complexity of drivers that interact together in determining the modifications of future communities. This study highlights the importance of appropriate selection of the modelling approaches and critical evaluation of the underlying assumptions in predicting future scenarios of community evolution under climate change. Starting from these outcomes, new future perspectives can be opened, as e.g. testing for the validity of macroecological constraints when modelling bird assemblages, or accounting for birds interactions to define assembly rules. In addition, trasferability tests (i.e. hindcasting to past or predicting from the past to the present, as similarly done in e.g. Araújo et al., 2005) could be used to comprehensively compare S-SDM and SESAM predictive abilities.

Author contributions

MDF, AG and MDA designed the study. DDR collected the data. MDF ran the analyses, and drafted the manuscript with the help of AG, MDA, PR and AL. All authors significantly contributed to editing and revising the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.10.023.

References

Algar, A.C., Kharouba, H.M., Young, E.R., Kerr, J.T., 2009. Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. Ecography (Cop.) 32, 22–33.

Allen, C.R., Pearlstine, L.G., Kitchens, W.M., 2001. Modeling viable mammal populations in gap analyses. Biol. Conserv. 99, 135–144.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232.

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J., Chunco, A.J., 2011. Do species' traits predict recent shifts at expanding range edges? Ecol. Lett. 14, 677–689.

Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. Glob. Ecol. Biogeogr. 16, 743–753.

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species–climate impact models under climate change. Glob. Chang. Biol. 11, 1504–1513.

Barbet-Massin, M., Thuiller, W., Jiguet, F., 2010. How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? Ecography (Cop.) 33, 878–886. https://doi.org/10.1111/j.1600-0587.2010.06181.x.

Barry, J.P., Baxter, C.H., Sagarin, R.D., Gilman, S.E., 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. Science 267 (80), 672–675.

Böhning-Gaese, K., Lemoine, N., 2004. Importance of climate change for the ranges, communities and conservation of birds. Adv. Ecol. Res. 35, 211–236.

Bradshaw, W.E., Holzapfel, C.M., 2006. Evolutionary response to rapid climate change. Science 312 (80), 1477–1478.

Breiner, F.T., Guisan, A., Bergamini, A., Nobis, M.P., 2015. Overcoming limitations of modelling rare species by using ensembles of small models. Methods Ecol. Evol. 6, 1210–1218. https://doi.org/10.1111/2041-210X.12403.

Bretagnolle, V., Gillis, H., 2010. Predator–prey Interactions and Climate Change. Eff. Clim. Chang. Birds. Oxford Univ. Press, Oxford, pp. 227–248.

Brito, D., Grelle, C.E.V., 2006. Estimating minimum area of suitable habitat and viable population size for the northern muriqui (Brachyteles hypoxanthus). Biodivers. Conserv. 15, 4197–4210.

Calabrese, J.M., Certain, G., Kraan, C., Dormann, C.F., 2014. Stacking species distribution models and adjusting bias by linking them to macroecological models. Glob. Ecol. Biogeogr. 23, 99–112.

Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-continuum concept. Oecologia 112, 143–149. https://doi.org/10.1007/s004420050293.

Cassey, P., Lockwood, J.L., Blackburn, T.M., Olden, J.D., 2007. Spatial scale and evolutionary history determine the degree of taxonomic homogenization across island bird assemblages. Divers. Distrib. 13, 458–466.

Chiatante, G., 2017. Landscape structure influencing the spatial distribution of the Short-toed Treecreeper *Certhia brachydactyla* in a Mediterranean agroecosystem. Avian Biol. Res. 10, 49–57. https://doi.org/10.3184/175815617X14836196626584.

Chiatante, G., Meriggi, A., 2016. The importance of rotational crops for biodiversity conservation in mediterranean areas. PLoS One 11, e0149323. https://doi.org/10.1371/journal.pone.0149323.

Cord, A.F., Klein, D., Gernandt, D.S., la Rosa, J.A.P., Dech, S., 2014. Remote sensing data can improve predictions of species richness by stacked species distribution models: a case study for Mexican pines. J. Biogeogr. 41, 736–748.

D'Amen, M., Dubuis, A., Fernandes, R.F., Pottier, J., Pellissier, L., Guisan, A., 2015a. Using species richness and functional traits predictions to constrain assemblage predictions from stacked species distribution models. J. Biogeogr. 42, 1255–1266. https://doi.org/10.1111/jbi.12485.

D'Amen, M., Mateo, R.G., Pottier, J., Thuiller, W., Maiorano, L., Pellissier, L., Ndiribe, C., Salamin, N., Guisan, A., 2017a. Improving spatial predictions of taxonomic, functional and phylogenetic diversity. J. Ecol. online ver. https://doi.org/10.1111/1365-2745.12801.

D'Amen, M., Pradervand, J.N., Guisan, A., 2015b. Predicting richness and composition in mountain insect communities at high resolution: a new test of the SESAM framework. Glob. Ecol. Biogeogr. 24, 1443–1453. https://doi.org/10.1111/geb.12357.

D'Amen, M., Rahbek, C., Zimmermann, N.E., Guisan, A., 2017b. Spatial predictions at the community level: from current approaches to future frameworks. Biol. Rev. 92, 169–187. https://doi.org/10.1111/brv.12222.

Di Febbraro, M., Carotenuto, F., Castiglione, S., Russo, D., Loy, A., Maiorano, L., Raia, P., 2017. Does the jack of all trades fare best? Survival and niche width in Late Pleistocene megafauna. J. Biogeogr. 44, 2828–2838. https://doi.org/10.1111/jbi.13078.

Di Febbraro, M., Roscioni, F., Frate, L., Carranza, M.L., De Lisio, L., De Rosa, D., Marchetti, M., Loy, A., 2015. Long-term effects of traditional and conservation-oriented forest management on the distribution of vertebrates in Mediterranean forests: a hierarchical hybrid modelling approach. Divers. Distrib. 21, 1141–1154. https://doi.org/10.1111/ddi.12362.

Diffenbaugh, N.S., Pal, J.S., Giorgi, F., Gao, X., 2007. Heat stress intensification in the Mediterranean climate change hotspot. Geophys. Res. Lett. 34, 1–6.

Douglas, D.J.T., Newson, S.E., Leech, D.I., Noble, D.G., Robinson, R.A., 2010. How important are climate-induced changes in host availability for population processes in an obligate brood parasite, the European cuckoo? Oikos 119, 1834–1840.

Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P., Guisan, A., 2011. Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. Divers. Distrib. 17, 1122–1131. https://doi.org/10.1111/j.1472-4642.2011.00792.x.

Elith, J., Kearney, M., Phillips, S.J., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

Fernandes, J.A., Cheung, W.W.L., Jennings, S., Butenschön, M., de Mora, L., Frölicher, T.L., Barange, M., Grant, A., 2013. Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. Glob. Chang. Biol. 19, 2596–2607. https://doi.org/10.1111/gcb.12231.

Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. J. Appl. Ecol. 43, 393–404. https://doi.org/10.1111/j.1365-2664.2006.01149.x.

Fornasari, L., De Carli, E., Brambrilla, S., Buvoli, L., Maritan, E., Mingozzi, T., 2002. Distribuzione dell'avifauna nidificante in Italia: primo bollettino del progetto di monitoraggio MITO2000. Avocetta 26, 59–116.

Gallien, L., Douzet, R., Pratte, S., Zimmermann, N.E., Thuiller, W., 2012. Invasive species distribution models - how violating the equilibrium assumption can create new insights. Glob. Ecol. Biogeogr. 21, 1126–1136. https://doi.org/10.1111/j.1466-8238.2012.00768.x.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends Ecol. Evol. (Amst.) 25, 325–331. https://doi.org/10.1016/j.tree.2010.03.002.

Gleason, H.A., 1939. The individualistic concept of the plant association. Am. Midl. Nat. 21, 92–110. https://doi.org/10.2307/2420377.

Guisan, A., Rahbek, C., 2011. SESAM - a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. J. Biogeogr. 38, 1433–1444. https://doi.org/10.1111/j.1365-2699.2011.02550.x.

Guisan, A., Theurillat, J.P., 2000. Equilibrium modeling of alpine plant distribution: how far can we go? Phytocoenologia 30, 353–384.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models: With Applications in R. Cambridge University Press, Cambridge, United Kingdom.

Hanley, J.A., McNeil, B.J., 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143, 29–36. https://doi.org/10.1148/radiology.143.1.7063747.

Hein, C.L., Öhlund, G., Englund, G., 2012. Future distribution of Arctic char Salvelinus alpinus in Sweden under climate change: effects of temperature, lake size and species interactions. Ambio 41, 303–312.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276.

Hof, A.R., Jansson, R., Nilsson, C., 2012. How biotic interactions may alter future predictions of species distributions: future threats to the persistence of the arctic fox in Fennoscandia. Divers. Distrib. 18, 554–562.

Hortal, J., De Marco Jr., P., Santos, A., Diniz-Filho, J.A.F., 2012. Integrating biogeographical processes and local community assembly. J. Biogeogr. 39, 627–628.

Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C., Willis, S.G., 2006. Potential impacts of climatic change upon geographical distributions of birds. Ibis (Lond. 1859) 148, 8–28.

Huntley, B., Collingham, Y.C., Willis, S.G., Green, R.E., 2008. Potential impacts of climatic change on European breeding birds. PLoS One 3, e1439.

IPCC, 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Knudsen, E., Lindén, A., Both, C., Jonzén, N., Pulido, F., Saino, N., Sutherland, W.J., Bach, L.A., Coppack, T., Ergon, T., 2011. Challenging claims in the study of migratory birds and climate change. Biol. Rev. 86, 928–946.

Lambert, D., 1992. Zero-inflated Poisson regression, with an application to defects in manufacturing. Technometrics 34, 1–14.

Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. Biometrics 33, 159–174.

Laughlin, D.C., Joshi, C., van Bodegom, P.M., Bastow, Z.A., Fulé, P.Z., 2012. A predictive model of community assembly that incorporates intraspecific trait variation. Ecol. Lett. 15, 1291–1299. https://doi.org/10.1111/j.1461-0248.2012.01852.x.

Lemoine, N., Bauer, H.-G., Peintinger, M., Böhning-Gaese, K., 2007. Effects of climate and land-use change on species abundance in a central European bird community. Conserv. Biol. 21, 495–503.

Lemoine, N., Böhning-Gaese, K., 2003. Potential impact of global climate change on species richness of long-distance migrants. Conserv. Biol. 17, 577–586.

Liu, C., Berry, P., Dawson, T., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography (Cop.) 3, 385–393.

Lomba, A., Pellissier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J., Guisan, A., 2010. Overcoming the rare species modelling paradox: a novel hierarchical framework applied to an Iberian endemic plant. Biol. Conserv. 143, 2647–2657. https://doi.org/10.1016/j.biocon.2010.07.007.

Maggini, R., Lehmann, A., Kéry, M., Schmid, H., Beniston, M., Jenni, L., Zbinden, N., 2011. Are Swiss birds tracking climate change?: detecting elevational shifts using response curve shapes. Ecol. Modell. 222, 21–32.

Maiorano, L., Falcucci, A., Zimmermann, N.E., Psomas, A., Pottier, J., Baisero, D., Rondinini, C., Guisan, A., Boitani, L., 2011. The future of terrestrial mammals in the Mediterranean basin under climate change. Philos. Trans. R. Soc. London. Ser. B 366, 2681–2692. https://doi.org/10.1098/rstb.2011.0121.

Mateo, R.G., Mokany, K., Guisan, A., 2017. Biodiversity models: what if unsaturation is

the rule? Trends Ecol. Evol. 32, 556–566. https://doi.org/10.1016/j.tree.2017.05.003.
Mateo, R.G.R.G., Felicísimo, Á.M., Pottier, J., Guisan, A., Muñoz, J., Felicisimo, A.M., Pottier, J., Guisan, A., Munoz, J., 2012. Do stacked species distribution models reflect altitudinal diversity patterns? PLoS One 7, e32586. https://doi.org/10.1371/journal.pone.0032586.
Mokany, K., Harwood, T.D., Williams, K.J., Ferrier, S., 2012. Dynamic macroecology and the future for biodiversity. Glob. Chang. Biol. 18, 3149–3159. https://doi.org/10.1111/j.1365-2486.2012.02760.x.
Møller, A.P., Saino, N., Adamík, P., Ambrosini, R., Antonov, A., Campobello, D., Stokke, B.G., Fossøy, F., Lehikoinen, E., Martin-Vivaldi, M., 2011. Rapid change in host use of the common cuckoo Cuculus canorus linked to climate change. Proc. R. Soc. Lond. B Biol. Sci. 278, 733–738.
Moreira, F., Russo, D., 2007. Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. Landsc. Ecol. 22, 1461–1476.
Morelli, F., Benedetti, Y., Ibáñez-Álamo, J.D., Jokimäki, J., Mänd, R., Tryjanowski, P., Møller, A.P., 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. Glob. Ecol. Biogeogr. 25, 1284–1293. https://doi.org/10.1111/geb.12486.
Newbold, T., Gilbert, F., Zalat, S., El-Gabbas, A., Reader, T., 2009. Climate-based models of spatial patterns of species richness in Egypt's butterfly and mammal fauna. J. Biogeogr. 36, 2085–2095.
Niehaus, A.C., Ydenberg, R.C., 2006. Ecological factors associated with the breeding and migratory phenology of high-latitude breeding western sandpipers. Polar Biol. 30, 11–17.
O'Connor, R.J., 1990. Some Ecological Aspects of Migrants and Residents. Bird Migration. Springer, pp. 175–182.
Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100.
Pellissier, L., Pradervand, J.N., Pottier, J., Dubuis, A., Maiorano, L., Guisan, A., 2012. Climate-based empirical models show biased predictions of butterfly communities along environmental gradients. Ecography (Cop.) 35, 684–692. https://doi.org/10.1111/j.1600-0587.2011.07047.x.
Pottier, J., Dubuis, A., Pellissier, L., Maiorano, L., Rossier, L., Randin, C.F., Vittoz, P., Guisan, A., 2013. The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. Glob. Ecol. Biogeogr. 22, 52–63. https://doi.org/10.1111/j.1466-8238.2012.00790.x.
Raes, N., 2012. Partial versus full species distribution models. Nat. Conserv. 10, 127–138.
Raia, P., Passaro, F., Fulgione, D., Carotenuto, F., 2012. Habitat tracking, stasis and survival in Neogene large mammals. Biol. Lett. 8, 64–66. https://doi.org/10.1098/rsbl.2011.0613.
Schaefer, H., Jetz, W., Böhning-Gaese, K., 2008. Impact of climate change on migratory birds: community reassembly versus adaptation. Glob. Ecol. Biogeogr. 17, 38–49.
Seoane, J., Justribo, J.H., García, F., Retamar, J., Rabadan, C., Atienza, J.C., 2006. Habitat-suitability modelling to assess the effects of land-use changes on Dupont's lark Chersophilus duponti: a case study in the Layna Important Bird Area. Biol. Conserv. 128, 241–252.
Sirami, C., Brotons, L., Burfield, I., Fonderflick, J., Martin, J.-L., 2008. Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biol. Conserv. 141, 450–459.
Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., Brotons, L., Martin, J.L., 2017. Impacts of global change on species distributions: obstacles and solutions to integrate climate and land use. Glob. Ecol. Biogeogr. 26, 385–394. https://doi.org/10.1111/geb.12555.
Smeraldo, S., Di Febbraro, M., Ćirović, D., Bosso, L., Trbojević, I., Russo, D., 2017. Species distribution models as a tool to predict range expansion after reintroduction: a case study on Eurasian beavers (Castor fiber). J. Nat. Conserv. 37, 12–20. https://doi.org/10.1016/j.jnc.2017.02.008.
Steinmann, K., Linder, H., Zimmermann, N.E., 2009. Modelling plant species richness using functional groups. Ecol. Modell. 220, 962–967. https://doi.org/10.1016/j.ecolmodel.2009.01.006.
Stephens, P.A., Mason, L.R., Green, R.E., Gregory, R.D., Sauer, J.R., Alison, J., Aunins, A., Brotons, L., Butchart, S.H.M., Campedelli, T., Chodkiewicz, T., Chylarecki, P., Crowe, O., Elts, J., Escandell, V., Foppen, R.P.B., Heldbjerg, H., Herrando, S., Husby, M., Jiguet, F., Lehikoinen, A., Lindström, Å., Noble, D.G., Paquet, J.-Y., Reif, J., Sattler, T., Szép, T., Teufelbauer, N., Trautmann, S., van Strien, A.J., van Turnhout, C.A.M., Vorisek, P., Willis, S.G., 2016. Consistent response of bird populations to climate change on two continents. Science 352 (80), 84–87. https://doi.org/10.1126/science.aac4858.
Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science 240 (80), 1285–1293.
Thuiller, W., F Midgley, G., Rougeti, M., M Cowling, R., 2006. Predicting patterns of plant species richness in megadiverse South Africa. Ecography (Cop.) 29, 733–744.
Tingley, M.W., Koo, M.S., Moritz, C., Rush, A.C., Beissinger, S.R., 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. Glob. Chang. Biol. 18, 3279–3290.
Van Turnhout, C.A.M., Foppen, R.P.B., Leuven, R.S.E.W., Van Strien, A., Siepel, H., 2010. Life-history and ecological correlates of population change in Dutch breeding birds. Biol. Conserv. 143, 173–181.
Vincent, P.J., Haworth, J.M., 1983. Poisson regression models of species abundance. J. Biogeogr. 153–160.
WCS - Wildlife Conservation Society, CIESIN - Center for International Earth Science Information Network - Columbia University, 2005. Last of the Wild Project, Version 2, 2005 (LWP-2). Global Human Footprint Dataset (IGHP).